14.—Description of a New Plesiosaur (Plesiosaurus capensis, sp. nov.) from the Uitenhage Beds of Cape Colony.—By C. W. ANDREWS, D.Sc., F.R.S., of the British Museum (Natural History).

(Plate XVIII., text-Figs. 1-4.)

In the Annual Report of the Geological Commission of the Cape of Good Hope for 1900 (1901) Messrs. Rogers and Schwarz* announced the discovery of the remains of a Plesiosaurian reptile, which were found by Mr. Schwarz in a cliff at Picnic Bush, in the valley of the Zwartzkops River, between Uitenhage and the sea. The deposit in which the fossil was, found is described as a nodular clay-limestone, and belongs to the Sunday River beds of the Uitenhage Series. The age of this series seems now to have been fairly definitely settled by Dr. Kitchin † as the Upper Velangian and Lower Hanterivian horizons of the Neocomian; that is to say, corresponding in age to some part, probably the upper, of the Wealden beds of England.

So far as I am aware, this is the first mention of the occurrence of a Plesiosaurian in South Africa. The discovery is afterwards again referred to in Rogers' and du Toit's "Introduction to the Geology of Cape Colony," p. 331 (2nd ed., 1909).

The specimens were entrusted to the late Professor H. G. Seeley for description, but unfortunately he died before any account of them had appeared. Afterwards, through the kindness of Dr. A. W. Rogers, the material passed into my hands, and the present paper contains the results of my examination of the remains.

Originally the bones seem to have been embedded in hard matrix at least to a large extent, but much of this has been successfully removed, and a considerable part of the skeleton is now visible. The parts preserved are—skull, part of the mandible, some teeth,

^{*} Appendix I., Report on the Survey of Parts of the Uitenhage and Port Elizabeth Divisions, p. 8.

[†] Kitchin, Ann. S. African Museum, vol. vii. (1908), "The Invertebrate Fauna and Palæontological Relations of the Uitenhage Series," p. 21.

limb bones, including portions of the femora, tibiæ, fibulæ, and a number of phalanges. These show that the animal was a typical Plesiosaur, and, in the absence of the pectoral girdle, I see no sufficient reason to regard it as other than a species of the genus Plesiosaurus. It will be shown below that it differs in several respects from other known species from approximately contemporary deposits, and it is therefore regarded as a new species, for which the name *Plesiosaurus capensis* is suggested.

The skull (Pl. XVIII., Fig. 1, text-Fig. 1) is in a fair state of preservation : nearly the whole of the palatal surface can be seen, but of the dorsal surface the greater part of the left side is concealed by the neural spines of six dorsal vertebræ which have been crushed down upon it. Part of the sub-orbital region of the right side and the right zygomatic arch are missing, and the zygoma of the left side is in part concealed by matrix. Between the temporal fossæ the parietals probably formed a well-marked sharp crest, but for the most part this has been broken away. The snout is narrow, and at the point where the maxillo-premaxillary suture crosses the alveolar border there is a slight constriction. The greatest width of the skull is between the outer ends of the quadrates, and this measurement is to the length of the skull from the occipital condyle to the tip of the snout, about as 2 to 3.

The basi-occipital (b.oc.) appears to bear the whole of the occipital condyle, which is sessile and considerably wider than high. Beneath the condyle there is a narrow vertical surface, running out laterally on to the posterior face of the postero-lateral (pterygoid) processes. The lower ends of these, and indeed the whole ventral face of the basi-occipital, are covered by the pterygoids, which meet in the middle line. It is not possible to make out the sutures between the basi-occipital and the exoccipital-opisthotics. The latter are, so far as can be seen, similar to the same elements in the other Plesiosaurs; that is to say, they consist of a columnar portion forming the sides of the foramen magnum and uniting above with the supraoccipital, and a long paroccipital process which runs outwards, downwards and backwards to the quadrate (q_{\cdot}) , with which its outer end was probably in contact, though possibly it joined the outer end of the quadrate process of the pterygoid, the sutures in this region being very indistinct.

The *supra-occipital* forming the upper part of the foramen magnum is crushed over to the left, and the shape of the opening thereby distorted. At its upper end the supra-occipital united with parietals, but its precise relations with those bones cannot be made out. As usual the posterior part of the parietals, probably together with the parietal processes of the squamosal, project some distance behind the occipital surface.

The basi-sphenoid is concealed by the overlapping pterygoids and by the posterior end of the parasphenoid. This latter (pas.) is a narrow vertical plate, not a horizontal one, as in *Murænosaurus* and *Cryptocleidus*. As in the other Plesiosaurs, it divides the posterior inter-pterygoid vacuity into two openings (p.i.v.) (elsewhere called the posterior palatine vacuities). Its anterior end is thrust between

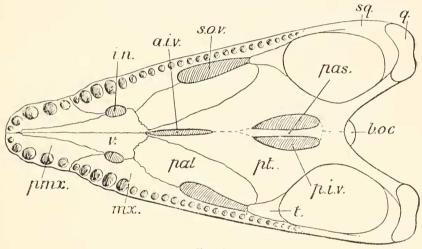


FIG. 1.

 Diagrammatic view of the palate of *Plesiosaurus capensis*. int. size.
 a.i.v., anterior interpterygoid vacuity; b.oc., basi-occipital; i.n., internal narial openings; mx., maxilla; pal., palatine; pas., parasphenoid; p.i.v., posterior inter-pterygoid vacuity; pmx., premaxilla; pt., pterygoid; q., quadrate; s.o.v., sub-orbital vacuity; t., transpalatine bone; v., vomer.

the palatine plates of the pterygoids, but its exact limits are obscure. The *pterygoids* (pt.) are of the usual triradiate form : posteriorly they unite with one another in the middle line beneath the basioccipital and basi-sphenoid, and are produced backwards and outwards into thin vertically compressed processes to the quadrates. In front of their union beneath the basis cranii the median borders of these bones diverge from one another and enclose a large oval inter-pterygoid vacuity (p.i.v.) which, as just mentioned, is divided into two in the middle line by the parasphenoid. In front of this vacuity the anterior end of this bone is wedged in between the

Annals of the South African Museum.

about twenty cervical and fifteen dorsal vertebrae, some imperfect pterygoids for a short distance; in front of this again the pterygoids meet in the middle line for a short distance, and then are separated by a narrow anterior inter-pterygoid vacuity (a.i.v.). Possibly they may be in contact with one another again at their anterior ends. The outer border of the posterior ramus in front of the union beneath the basis cranii runs forwards and at first slightly outwards, then turning outwards almost at right angles to form the posterior border of the lateral ramus. The outer end of this joins the transpalatine bone (t.) which connects the pterygoid with the maxilla. The flat anterior ramus of the pterygoid is broad posteriorly but narrows towards its anterior end, where it joins the vomers (prevomers). On its outer side it joins the palatine in a long oblique suture.

The palatine (pal) is an elongated bone, the inner border of which, as just described, unites in suture with the pterygoid. Anteriorly the palatines converge, but do not seem to meet owing to the union of the anterior ends of the pterygoids with the vomers; at the same time it should be noted that in this specimen the sutures are not very distinct. The rounded anterior ends of the palatines unite with the vomers, externally to these they join the palatine plates of the maxilla, for a short distance behind which they are separated from that bone by a narrow sub-orbital vacuity (s.o.v.), which is closed posteriorly by the transpalatine bone (t.), with which the hinder end of the palatine unites. The transpalatine bone (t.) is a triradiate element, its outer side unites with the maxilla, its inner branch underlies the outer end of the lateral ramus of the pterygoid, and its anterior concave border is in contact with the palatine, its anterior angle closing the sub-orbital vacuity (s.o.v.) posteriorly.

The vomers (v.) (prevomers of Broom) are closely united with one another in the middle line, the original suture between them being only visible in their expanded posterior portion. The united bones extend far forwards between the premaxillæ, almost to the pits occupied by the tips of the replacing teeth. Followed back to the nares (i.n.), they widen gradually and are convex from side to side; at the nares they are again narrowed and the palatal surface becomes flat. Behind the nares they widen out into a fan-like expansion, and, as already mentioned, the suture between them is visible, and is situated at the bottom of a median depression. In front of the nares the vomers lie between the palatine plates of the premaxillæ, which extend back just to the anterior angle of the narial opening (i.n.). Behind the nares they unite with the palatine plates of the maxilla externally, internal to this with the palatines, and in the middle line probably with the anterior ends of the pterygoids, though this is not quite clear.

The premaxillæ (pmx.) which form the narrow muzzle, each bear alveoli for five teeth. Of these the anterior one is small and close to the middle line; the second is rather larger; both these teeth seem to have been directed forward. The third and fourth teeth are large, the fifth again smaller. Immediately behind the last there is a short diastema crossed by the maxillo-premaxillary suture. Within the row of alveoli and separated from them by a flattened area there is a row of pits which mark the points at

Owing to a regrettable printer's error a line has been misplaced in Dr. C. W. Andrews' paper, Annals S. Afr. Museum, Vol. VII. Part 4.

The parts preserved are—skull, part of the mandible, some teeth, about twenty cervical and fifteen dorsal vertebræ, some imperfect limb bones, including portions of the femora, tibiæ, fibulæ, &c.

be seen, however, that the first tooth was small, while the succeeding three were greatly enlarged, the third being the largest. The palatine portion of the bone is in contact with the premaxilla in front; behind this it forms the outer border of the internal nares; behind this again it joins the palatine for some distance, but posteriorly is separated from it by the narrow sub-orbital vacuity (*s.o.v.*). Behind this it unites with the transverse bone and posteriorly probably with the jugal. The facial surface is imperfectly preserved : the maxillo-premaxillary suture runs from the alveolar border upwards and backwards, then backwards nearly parallel with the middle line as far as the external nares which form deep notches in the border of the premaxillæ. The relations of the facial region of

Annals of the South African Museum.

about twenty cervical and fifteen dorsal vertebræ, some imperfect pterygoids for a short distance; in front of this again the pterygoids meet in the middle line for a short distance, and then are separated by a narrow anterior inter-pterygoid vacuity (a.i.v.). Possibly they may be in contact with one another again at their anterior ends. The outer border of the posterior ramus in front of the union beneath the basis cranii runs forwards and at first slightly outwards, then turning outwards almost at right angles to form the posterior border of the lateral ramus. The outer end of this joins the transpalatine bone (t.) which connects the pterygoid with the maxilla. The flat anterior ramus of the pterygoid is broad posteriorly but perserve

consistent in the matuale line, the original suture between them being only visible in their expanded posterior portion. The united bones extend far forwards between the premaxillæ, almost to the pits occupied by the tips of the replacing teeth. Followed back to the nares (i.n.), they widen gradually and are convex from side to side; at the nares they are again narrowed and the palatal surface becomes flat. Behind the nares they widen out into a fan-like expansion, and, as already mentioned, the suture between them is visible, and is situated at the bottom of a median depression. In front of the nares the vomers lie between the palatine plates of the premaxillæ, which extend back just to the anterior angle of the narial opening (i.n.). Behind the nares they unite with the palatine plates of the maxilla externally, internal to this with the palatines, and in the middle line probably with the anterior ends of the pterygoids, though this is not quite clear.

The premaxillæ (pmx.) which form the narrow muzzle, each bear alveoli for five teeth. Of these the anterior one is small and close to the middle line; the second is rather larger; both these teeth seem to have been directed forward. The third and fourth teeth are large, the fifth again smaller. Immediately behind the last there is a short diastema crossed by the maxillo-premaxillary suture. Within the row of alveoli and separated from them by a flattened area there is a row of pits which mark the points at which the replacing teeth appear. Internal to the two posterior pits the surface of the premaxilla is raised into a ridge on a level with the vomer against which it abuts. The facial surface of the premaxillæ consists of a broad anterior region, convex from side to side with a median groove marking the line of union of the two bones, and a backwardly prolonged narrow facial process, the two bones uniting in this region to form a prominent ridge with concave sides which extends back between the orbits: how far back the facial processes of the premaxillæ extend cannot be determined from this specimen, but probably, judging from what occurs in some of the Oxford Clay genera, they joined the frontals a little in front of the level of the posterior border of the orbits. It is possible that these backward prolongations of the premaxillæ may, as suggested by Williston, include some other element, possibly the nasal, though I have never seen any evidence of this. The upper surface of the anterior part of the premaxillæ is much roughened and bears a number of vascular foramina.

The maxilla (mx.) is not completely preserved on either side of the skull, and it is not possible to say how many teeth it bore; it can be seen, however, that the first tooth was small, while the succeeding three were greatly enlarged, the third being the largest. The palatine portion of the bone is in contact with the premaxilla in front; behind this it forms the outer border of the internal nares; behind this again it joins the palatine for some distance, but posteriorly is separated from it by the narrow sub-orbital vacuity (s.o.v.). Behind this it unites with the transverse bone and posteriorly probably with the jugal. The facial surface is imperfectly preserved : the maxillo-premaxillary suture runs from the alveolar border upwards and backwards, then backwards nearly parallel with the middle line as far as the external nares which form deep notches in the border of the bones, their inner edge being formed by the facial processes of the premaxillæ. The relations of the facial region of

the maxillæ to the bones behind cannot be made out, and it is uncertain whether there is a lachrymal, a pre-frontal, or a nasal. Probably the bone forming the anterior part of the raised rim of the roof of the orbit was the pre-frontal, while that forming the posterior part was the post-frontal, but no sutures are visible. Neither can sutures be seen between the frontals and the surrounding bones. The pineal foramen seems to have been just opposite the anterior border of the temporal fossæ and probably marks the anterior limit of the parietal bones. These formed a high, narrow, sagittal crest between the temporal fossæ, but in this specimen its summit is broken away. Posteriorly these bones widen out and project backwards behind the level of the foramen magnum; how far the lateral expansions of the parietals are overlapped by the upper limbs of the squamosals cannot be determined. The ventral process of the squamosal (sq.) can be seen to be closely adherent to the posterior and outer face of the large quadrate (q_i) extending far down its side. The zygomatic process seems to have been wide, but the relations of its anterior end to other bones cannot be seen. The quadrate (q_{\cdot}) is relatively very large : its anterior face is concave from side to side, while its posterior face is convex in the same direction. The articular surface for the mandible is imperfect, but must have been very wide, as is shown also by the width of the articular surface of the mandible. The outer face of the quadrate, as already mentioned, was overlapped by the ventral process of the squamosal, while the inner side unites with the quadrate ramus of the pterygoid and probably also with the outer end of the paroccipital process of the opisthotic, though possibly this only supports the quadrate through the medium of the pterygoid.

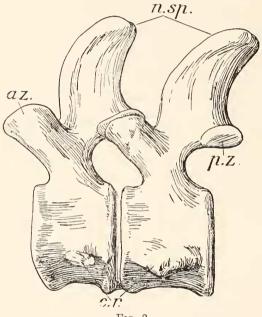
The manifible (Pl. XVIII., Figs. 2, 3) is only imperfectly preserved, the symphysial region being completely wanting. It seems to have been very strongly built for the size of the skull. The articulation for the quadrate is very broad; it consists of two concave surfaces, the inner being the larger, separated by a slight convexity: both in front and behind it is bordered by a strongly raised rim, so that the articulation must have been a very strong one. On the outer side of the jaw, just beneath the articular surface, there is a deep and roughened pit or groove, apparently for the attachment of ligament. The post-articular process is short and broad; its inner border is rounded, while the outer forms a sharp edge. Its upper portion is formed by the hinder part of the united surangular and articular bones (Pl. XVIII., Figs. 2 and 3, s. ang. and art.), the lower portion is constituted by the angular (Fig. 3, ang.). In

front of the articular surface the upper border, formed by the united surangular and articular, rises to a blunt coronoid angle where it meets the dentary on its outer side and the coronoid (cor.) on the inner; the anterior limits of the coronoid are not known, but it seems to have extended as a thin plate, closely adherent to the inner face of the dentary, forwards to about the level of the middle of the dental series. The greater part of the dentigerous part of the mandible is formed, as usual, by the dentary, which is the only element visible on the outer side of this part of the jaw. On its inner face the upper part of the posterior end is covered by the closely adherent coronoid, while beneath this is the thin plate-like splenial (spl.) which closes Meckel's groove, and probably extended forward to the symphysis into the formation of which it perhaps entered: posteriorly it is prolonged back some distance behind the level of the coronoid angle, forming the lower (inner) edge of the opening of the dental (Meckel's) canal. Beneath the splenial and on the inner side of the dentary the angular sends forward a long tapering process, the anterior end of which is concealed by the overlap of the splenial upon the dentary. In the neighbourhood of the symphysis the dentary widens out and bears at least three greatly enlarged teeth: behind these the teeth are smaller and continue about equal in size for the first six or seven: behind these again there is a gradual reduction in size to the end of the series. The outer face of the dentary is marked by numerous vascular grooves and foramina.

Several teeth (Pl. XVIII., Fig. 4) are preserved, differing much in size and to some extent in shape. The larger ones have long conical, slightly curved crowns, circular in section and probably terminating in a sharp point. On the inner (concave) side of the crown the enamel is raised into numerous fine longitudinal ridges which tend to unite with one another in pairs as they are followed towards the tip of the crown; similar ridges occur to a less extent on the anterior and posterior faces of the crown, but on the outer (convex) face the enamel is almost smooth, only a very faint ridging being visible. The roots of the teeth are very large, smooth and circular in section. In the smaller teeth (Pl. XVIII., Fig. 4) the crown is more strongly curved. The enamel ridges are relatively larger and fewer in number, but their arrangement is the same as in the large teeth.

Of the vertebral column (Pl. XVIII., Figs. 5, 6; text-Figs. 2, 3) a considerable portion is preserved. Twenty-one or twenty-two cervicals are present, of which eleven are anterior, the remainder posterior and forming a continuous series with the fifteen pectorals

and dorsals that are preserved. In the anterior cervicals (Pl. XVIII., Figs. 5, 6) the centra are considerably wider than long; their articular faces are wider than high and are deeply concave, the centre being occupied by a large sharply defined fossa (Fig. 6). This depression seems to be more deeply excavated on the posterior than on the anterior face, and is particularly sharply defined in the more anterior vertebræ. In these also the centra bear a sharp hypa-





2. Posterior cervical vertebræ of *Plesiosaurus capensis*; from left side. About $\frac{2}{3}$ nat. size.

a.z., anterior zygapophysis; *c.r.*, bases of cervical ribs; *n. sp.*, neural spine; p.z., posterior zygapophysis.

pophysial ridge (Fig. 5*a*), which is as it were pinched up and has on either side of it a concave surface; near its anterior end there are in some cases small sharp lateral projections which probably served for the insertion of tendons. On either side of the ridge and close to it are the nutritive foramina. The cervical ribs are fused with the ventro-lateral borders of the centra, and above them the sides of the centra are concave both from side to side and from above downwards. The neural arch is high and is fused with the centrum; the

316

317

zygapophyses are relatively large; the neural spines are incomplete in all the anterior cervicals. In the posterior cervicals (text-Fig. 2) the hypapophysial ridge is broadly rounded, and is best marked in the anterior part of the centrum; the ventral nutritive foramina are here separated by an interval of about 1.5 cm. It is possible that some of the posterior cervical ribs were still free. In this region the zygapophyses are large and the anterior ones project strongly forwards. The neural spines, which are not very high, slope backwards; their anterior border is convex, the posterior concave. In the hindermost cervicals the rib-facet passes up on to the arch, but the condition of the specimen makes it difficult to determine in which the passage actually takes place; probably the tenth and eleventh of the series as preserved may be regarded as the transitional (pectoral) vertebræ.

The dorsals (text-Figs. 3A, 3B) have the centra relatively shorter than the cervicals and at the same time rounder, the transverse diameter being little greater than the vertical. The ventral surface of the centrum is almost evenly rounded from side to side, there being only a slight trace of a hypapophysial ridge, on either side of which are the nutritive foramina (n, f'). The upper part of the sides of the vertebræ is concave in all directions; the lower border of the concavity approximately marks the line of the suture between the centrum and the arch; at its lower angle there is a vascular foramen (n.f.). The articular ends of the centrum are nearly circular except for the presence of a slight depression beneath the neural canal; they are fairly deeply concave but without the sharp central depression seen in the cervicals; their outer edges are sharp and well defined. The neural arches are lower than in the cervical region and the zygapophyses are proportionately smaller; the anterior zygapophyses (a.z.) project considerably forwards, the whole of their articular surface lying in front of the centrum. A strong ridge runs from the anterior zygapophysis to the anterior border of the transverse process, which in the anterior dorsals is situated low down on the arch but passes upwards as the series is followed back; it is compressed from above downwards. The height of the neural spines (n.sp.) in the dorsal region is not known, all having been broken off short.

Of the limbs (text-Fig. 4) there remain portions of two paddles, which I regard as posterior. One consists of the much-shattered and imperfect distal portion of the femur with the tibia and fibula attached. The other is the upper part of the shaft of the other femur and the detached tibia and fibula, in excellent preservation,

Annals of the South African Museum.

there is also a carpal, probably a fibulare, and a number of phalanges, which cannot be placed. The femur seems to have possessed a welldeveloped trochanter, and on the ventral face of the shaft there was a rugose surface for the attachment of muscles; distally it expanded considerably (text-Fig. 4, *fem.*); indeed, its expansion seems to have

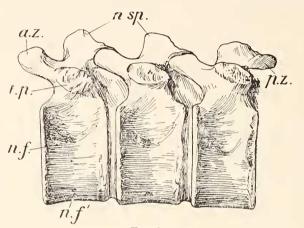
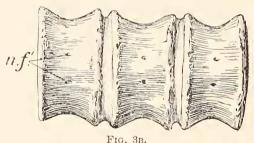


FIG. 3A.

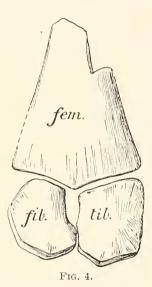


IIG. OD.

3. Dorsal vertebræ of *Plesiosaurus capensis* : A. from left side, B. from below. $\frac{2}{3}$ nat. size.

a.z., anterior zygapophyses; n.f. and n.f.'; nutritive foramina; n. sp., neural spine; p.z., posterior zygapophysis; t.p., transverse processes.

been too great for articulation with the tibia and fibula only, and probably it also supported a posterior accessory ossicle. The tibia and fibula (text-Fig. 4, *tib. fib.*) are more elongated than one would expect to find them in a Wealden form, and in this respect the paddle much resembles that of some of the Lower Lias Plesiosaurs, *e.g.*, *P. hawkinsi*. The tibia (*tib.*) articulates with the femur by a long and slightly convex facet; its anterior border is sharp and almost straight, while the post-axial border is concave in its proximal half but distally is occupied by a large facet for union with the fibula, with which there seems to have been no contact at the proximal end. Distally there is a long, flat facet for the tibiale; in front of this there is a small, oblique facet and behind it a longer, also oblique facet for the intermedium. The fibula (*fib.*) is a kidney-shaped bone; proximally it bears a large, nearly straight surface for union with the femur; anteriorly it has in its proximal portion a concave,



 Portion of hind paddle of *Plesiosaurus capensis*. About ¹/₃ nat. size. fem., femur; fib., fibula; tib., tibia.

sharp-edged border and distally a facet for union with the tibia. The remainder of the border is occupied by four facets—one for the intermedium, behind this a surface for the fibulare, next a postaxial surface looking nearly directly backwards, and lastly a small surface looking upwards and backwards, which probably supported an accessory ossicle which also articulated with the femur. The chief peculiarity of this tibia and fibula, apart from their length, is that, although they unite distally, proximally there is a considerable interval between them which is only closed above by the humerus. I am not acquainted with any Plesiosaur in which exactly the same thing is seen; usually in the post-Liassic Plesiosaurs the tibiæ and fibulæ are much shortened, and if there is any interval between them, it is a small foramen or slit which is enclosed above and below by the meeting of these bones.

For comparison of this species with previously described species from the same or approximately the same horizon the cervical vertebræ are of the greatest importance, since the skull is quite unknown in the other species and only a few odd limb bones have hitherto been found. The cervical vertebræ are very similar to those of some of the nearly contemporaneous forms, particularly in the presence of a sharply defined and deep central depression in the middle of the more gently concave articular surfaces of the centra, but in all cases differences are apparent which forbid the inclusion of this form in any of the species hitherto described.

The forms which seem to resemble the present species most nearly are *Plesiosaurus degenhardti* Koken, *P. limnophilus* Koken, and *P. valdensis* Lydekker, sp.; there is also a certain amount of similarity to *P. bernardi* Owen and some other species.

In Plesiosaurus degenhardti^{*} of Koken the form of the centra of the cervicals differs considerably, the height of their centra being greater than either their width or length; in the present species the width is the greater, and at the same time in *P. degenhardti* the edges of the articular surfaces are more rounded and thickened and the zygapophyses are smaller. The difference in the proportions of the centra is shown if we compare centra of approximately the same size of the two species: thus, in the present species, if the length of the centrum be taken as 100, the width will be about 156, the height 138; while in *P. degenhardti*, the length being 100, the width will be 127, the height 152.

From *Plesiosaurus limnophilus* \dagger of Koken the difference is also well marked, the length of the centrum being about equal to the width, while in *P. capensis* it is much less. In a vertebra from the Wealden of Cuckfield, Sussex, ascribed by Lydekker \ddagger to *P. limnophilus*, but regarded by Koken as probably distinct, the length and height of the centrum are about equal, but the width is greater. Comparison with *Plesiosaurus valdensis* \$ shows a much more marked similarity; in this case, the length of the centrum being taken as 100, the width is 151, the height 129—proportions which

320

^{*} Koken, Palæont. Abhandl., vol. iii. (1887), p. 414; see also vol. vii. (1896), p. 122, pl. iii.

[†] Koken, op. cit., vol. iii. (1887), p. 417.

[‡] Lydekker, Catal. Foss. Rept. Brit. Mus., pt. ii. (1889), p. 224.

[§] Lydekker, tom. cit., p. 188.